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Diel Movements of Resident and Transient Zooplankters Above Lagoon Reefs at Enewetak Atoll, Marshall Islands[1]

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ABSTRACT: Of those zooplankters above reefs on the lagoon shelf at Enewetak Atoll at some time during the diel cycle, the vast majority of those larger than about 1.5 mm were there only at night. Many of these larger forms were local residents that by day sheltered in or near shelf substrata, or in swarms close to these substrata, and at night made purposeful forays above the shelf. Many others, however, were transients from the deeper regions of the lagoon, or from the open sea outside the atoll, and these were above the shelf at night by chance. The residents included various polychaetes, cypridinacean ostracods, copepods, mysids, tanaids, isopods, amphipods, and carideans. The transients were mostly holoplankters that included halocyprid ostracods, calanoid copepods, euphausids, and chaetognaths. Both residents and transients were above the shelf at night as a result of diel vertical migrations. The residents were adapted to stay within reach of their diurnal habitats while in the nocturnal water column, often by avoiding currents, and so were readily able to return to those habitats at dawn. The open-water transients, however, lacked such adaptations, and, as a result, probably many were stranded in the shallows above the shelf at dawn, unable to return to their daytime depths and probably vulnerable to planktivorous fishes.

ASSEMBLAGES OF ZOOPLANKTERS above tropical reefs differ from day to night. Most of these differences stem from diel movements of organisms that rise or disperse in the water column only after dark (see Emery 1968; Hobson and Chess 1978). Some of these nocturnal forms are residents of the reef area, whereas others are transients from other habitats. Diel patterns in each of the two groups are distinctive. By day most of the residents are either benthonic (Alldredge and King 1977; Hobson and Chess 1979) or aggregate in dense swarms close to benthic substrata (Hamner and Carleton 1979). The transients, in contrast, are mostly offshore holoplankters that are carried or disperse shoreward after rising toward the surface at night from deeper water (Hobson and Chess 1978).

Although these diel patterns are apparent from existing literature, there remains need for study at the species level in specific environments. Here we consider the patterns as they occur among zooplankters in the lagoon at Enewetak Atoll (11°26′N, 162°22′E). The study concerns those organisms that at some time during the diel cycle occurred above the shelf of sand and isolated patch reefs on the windward side of the lagoon. We consider all the varied forms which were collected in our plankton nets or traps and which belong to groups included in most general accounts of the zooplankton (such as Newell and Newell 1963; Wickstead 1965).

The goals of the study were twofold: to define the diel patterns of occurrence of zooplankters above patch reefs on the lagoon shelf and to determine which of them were residents of the shelf habitat and which were transients from the open sea or the deeper waters of the lagoon.

COLLECTING SITES

We sampled the zooplankton on the windward side of the lagoon where the shelf is one

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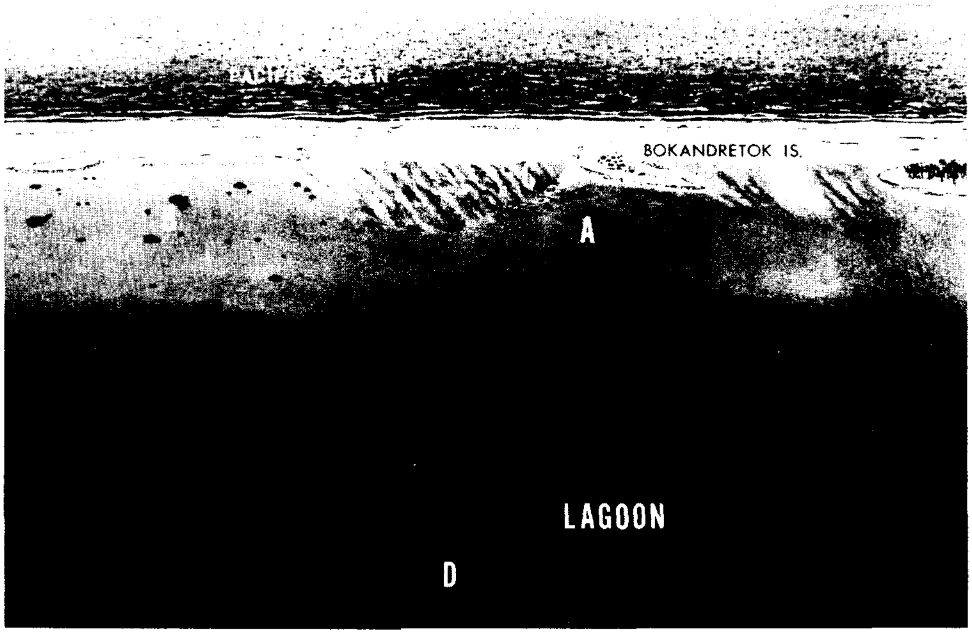

FIGURE 1. The study area on the windward lagoon shelf at Enewetak Atoll, with collecting stations designated. Station A is in the path of intermittent currents that bring water from the open sea across a low point in the interisland reef. Station B is protected from such currents by a high point on the interisland reef that remains exposed even at high tide. Station C is on the interisland reeftop, upcurrent from Station A. Station D is offshore in the lagoon, beyond the shelf.

to several hundred meters wide and under 5 to 15 m of water (Figure 1). At the outer edge of the shelf the bottom falls away sharply to depths of 30 to 50 m, which is the approximate water depth over much of the lagoon. Currents over the shelf consist of water that has flowed across the interisland reef from the open sea. This cross-reef flow is variable, depending on the height of the tide and the surf breaking on the ocean side, but it moves in just one direction—into the lagoon (Atkinson et al. 1981).

Zooplankton were sampled at or near four stations (Figure 1): Stations A and B were above the shelf, Station C was above the interisland reef, and Station D was in the deeper water of the lagoon, beyond the shelf. The collections at and near Stations A and B determined the composition of zooplankton assemblages above the lagoon shelf at different periods of the diel cycle. Because the distribution of these zooplankters was certain to be influenced by water currents, the two stations were positioned to sample contrasting examples of the highly variable current conditions that prevailed above the shelf.

Station A, which faced a low section of the interisland reef across which water flowed from the open sea during higher tides, was intermittently swept by currents of up to 25 cm/sec^{-1}. Although usually this flow was blocked by the exposed reef at low tide, even on the lowest tides the trade winds, or high seas breaking outside the atoll, sometimes drove enough water across the reef to generate currents on the shelf. When the wind shifted just a few degrees to the south, however, the current was deflected northward by Bokandretak Island, and Station A was in an extensive area of quiet water that persisted in the lee of that island (Figure 1). Station A encompassed a pair of patch reefs (both approximately 5 × 10 m), a few meters apart, in about 5 m of water.

Station B was sheltered from tidal currents by a high section of the interisland reef that was above water at all stages of the tide (Figure 1). Generally we were unable to detect a current at this station, although a lagoonward drift of a few cm/sec^{-1} sometimes was evident above the shelf a short distance offshore when high tides were backed by the usual strong trade winds. The station encompassed a pair of patch reefs (approximately 3 × 5 × 5 and 3 × 5 × 15 m), just a few meters apart, in about 5 m of water.

Station C was in water flowing across the interisland reef from outside the atoll on the higher tides and thus sampled the zooplankters that were entering the lagoon from the open sea.

Station D was in the deeper waters of the lagoon, and here we sampled zooplankters during the day to identify species likely to be among those from that habitat which joined the zooplankton above the shelf after dark.

COLLECTING METHODS

Most of the collections were made using SCUBA, so that we directly observed the conditions under study. And because the work was concentrated during 3 weeks of May and June 1979, we avoided many of the variables associated with changing seasons, such as seasonal differences in species composition (as reported from Enewetak by Gerber 1981).

To sample organisms in the water column (except at Station C), we pushed a net mounted in a square frame (78 × 78 cm) over an established course, each time for 10 min at a speed of about 30 cm/sec^{-1} (Hobson and Chess 1976, 1978), so that each of the collections filtered about 110 m^3 of water. The 0.333-mm mesh of this net, however, did not effectively sample zooplankters smaller than about 1 mm. Hence to gain some measure of organisms lost through the mesh of our standard net, we paired it in a limited number of collections with a net of 0.165-mm mesh set in a 0.5-m ring. Our standard net had the square frame rather than the usual circular frame because the square configuration was more effective close to the sea floor and the water's surface—two important concerns when sampling shallow-water zooplankton (Hobson and Chess 1978: fig. 2).

Because we swam with the nets during most of the collections, guiding them throughout, we sampled precisely defined locations and were able to observe many of the organisms in the path and immediate vicinity of the net. Thus we knew whether or not certain of the larger, more mobile organisms evaded our net. Mysids, for example, were among the more elusive forms, but even these escaped less often than might be expected owing to their mobility. Much of the time our net enveloped mysids without eliciting an evasive response, probably because the net's approach was relatively slow and quiet and its opening was unobstructed by the tethering gear that usually precedes a plankton net. We considered the unobstructed opening more important than an absolute measure of the volume of water filtered and thus did not use a flowmeter. The questions asked demanded only that the collections be comparable with each other, and this demand was met.

To identify those primarily benthic organisms that periodically left the shelf floor and joined the zooplankton, we placed traps on the three major shelf substrata—sand, rubble, and patch reef—in the vicinity of Stations A and B (Figure 2).

The traps used in sand and rubble were identical to the trap illustrated earlier (Hobson and Chess 1979: figs. 1 and 2; see that paper for details on how the traps worked), but these devices were unsuitable for use on the hard, irregular surfaces of the reef because their rigid metal bases required a bed of sediment. To sample the patch reefs, we used a trap that had as a base a pliable canvas skirt that could be folded over to form a continuous pocket. Once the base was in position on the reef, we loaded the pocket with bags of lead shot (approximately 18 kg) and then sealed it by adjoining a series of Velcro strips sewed to its edges. The base, which now matched the contours of the reef (and thus made a good seal with the reef), also provided an effective anchor (Figure 2: trap on the right).

Additional information on the sampling stations and the collection procedures is given below, where each element of the study is recounted in detail.

DIEL OCCURRENCES OF THE ZOOPLANKTERS ABOVE THE LAGOON SHELF

To characterize the diel occurrences of zooplankters above the lagoon shelf, we made ten pairs of collections with the standard plankton net at Stations A and B: four pairs by day and six pairs at night—a total of 20 collections. Each pair consisted of a collection at one station followed within 30 min by a collection at the other. At each station we always followed the same course, continously moving up and down between surface and bottom. The nocturnal collections were made without diving lights, because these are known to attract certain zooplankters and because natural light in these clear waters over white sand was sufficient to navigate even on moonless nights. The collections sampled day and night during high and low spring tides and also high and low neap tides. They also spanned all periods of the night, from 1 hr after sunset to 1 hr before sunrise, and through that part of the lunar cycle from new moon to three-quarter moon. The daytime collections were made between 1030 and 1600 hr.

These collections (Table 1) were judged to document the diel occurrences of zooplankters of about 1 mm in size and larger. Zooplankters smaller than this were poorly sampled by our standard net, however, a fact made clear by collections that paired this net with one of finer mesh (Table 2). So the material that follows, except where specified, refers to zooplankters 1 mm in size and larger.

At both stations, many more zooplankters were taken at night than during the day (Wilcoxon two-sample test: $Z = -3.67$, $p = 0.0001$). Furthermore, virtually all of the zooplankters larger than 2 mm in their greatest dimension were in the nocturnal collections. Included were species that belong to groups widely recognized as benthonic during much of the diel cycle, such as polychaetes, mysids, cumaceans, tanaids, isopods, amphipods, and natantians. Also included were species of groups widely considered to be in the water column throughout the diel cycle, such as calanoid copepods and chaetognaths. It was clear that during the day most of the larger zooplankters were somewhere other than in the water column above the lagoon shelf. It was equally clear that many smaller zooplankters (< 1 mm) did not follow this pattern, as they were abundant in these waters day and night (Table 2).

Had these collections been made with nets deployed from a vessel there would have been uncertainty whether the absence of larger (and therefore more mobile) forms meant they were in fact absent from the water column or whether daylight had simply allowed them to evade the net. But our direct observations in the environment throughout the diel cycle confirmed the collection results: the larger zooplankters generally were present in the water column above the shelf only at night.

Thus a major question was: where were the larger zooplankters during the day? Having identified the three obvious possibilities earlier (Hobson and Chess 1978), we set out to determine which of them had arrived above the patch reefs at night from daytime positions in, on, or close above the shelf, which of them had come over the interisland reef from the open sea, and which had come from the deeper waters of the lagoon.

ZOOPLANKTERS THAT SHELTERED ON THE SHELF

Our traps set on shelf substrata within 50 m of Stations A and B sampled organisms that entered the water column at some time during the diel cycle from benthic habitats on the shelf. The collections involved sets of three traps placed close together, each trap sampling one of the three major substrata: sand, rubble, and reef (Figure 2). Although the trap collections were designed to sample the major benthic habitats on the shelf, they did not effectively distinguish organisms associated with specific substrata. Only the sand collections represented what approximated a single substrate type. The rubble collections actually sampled a combination of rubble and sand, whereas the reef collections sampled combinations of all three substrata.

TABLE 1

Zooplankters Collected Above the Lagoon Shelf at Enewetak Atoll, Day and Night[*]

	DAY					NIGHT				
		STATION A (INTERMITTENT CURRENT) $N = 4$		STATION B (NO CURRENT) $N = 4$			STATION A (INTERMITTENT CURRENT) $N = 6$		STATION B (NO CURRENT) $N = 6$	
ORGANISM	SIZE (mm)	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.	SIZE (mm)	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.
Foraminiferans	0.3–1.5	100	61.1	100	17.3	0.3–1.5	100	232.4	100	100.9
Tretomphalus sp.	0.4–0.8	100	22.5	25	1.2	0.4–0.8	100	191.3	100	77.0
Discorbis sp.[†]	0.3–0.5	100	33.5	100	15.0	0.3–0.5	100	29.7	100	13.7
Cymbaloporella sp.	1.0–1.5	—	—	—	—	1.0–1.5	17	0.3	50	1.6
Globigerina sp.	0.3–0.4	75	4.5	50	0.8	0.3–0.4	33	0.3	50	2.3
Others	0.3–1.0	25	0.6	25	0.3	0.3–1.0	100	10.8	100	6.3
Polychaetes	—	—	—	—	—	0.5–12.0	100	27.0	100	22.4
Opheliids	—	—	—	—	—	3.0–12.0	50	23.0	33	11.5
Nereid epitokes	—	—	—	—	—	4.0–6.0	—	—	17	1.3
Undetermined	—	—	—	—	—	0.5–8.0	50	4.0	67	9.6
Veligers	0.4–1.2	100	57.3	75	4.0	0.4–1.3	100	37.0	100	32.3
Ostracods	0.8–1.5	25	0.5	25	0.5	0.5–3.0	100	80.5	100	95.6
Cypridinaceans	0.8–1.5	25	0.5	—	—	0.5–3.0	100	78.8	100	95.6
Halocyprids	—	—	—	25	0.5	1.0	33	1.7	—	—
Calanoids	0.8–2.0	100	44.8	100	17.8	0.7–4.0	100	422.8	100	1249.0
Acartia negligens	1.0	100	22.3	100	11.8	1.0	83	22.0	83	17.8
Undinula vulgaris	2.0	—	—	17	0.5	2.5–3.5	83	259.7	83	147.0
Calanopia minor	1.5	—	—	17	0.3	1.1–1.3	100	28.3	100	1013.0
Eleven others[‡]	0.8–1.5	50	1.3	50	1.3	1.5–4.0	83	69.5	100	46.5
Undetermined	1.0–2.0	100	21.2	50	4.9	0.7–3.0	67	43.3	100	24.7
Cyclopoids	0.7–2.0	100	19.8	100	6.4	0.8–1.5	83	16.4	83	17.3
Corycaeus sp.	0.7–1.0	100	16.3	50	1.3	0.8–1.0	50	13.3	17	14.0
Oncaea sp.	1.0	—	3.0	—	—	1.0	17	0.7	17	1.0
Oithona sp.	1.0	—	—	50	4.8	1.0	33	1.7	17	1.0
Sapphirina sp.	1.2–2.0	50	0.5	25	0.3	1.0–1.5	17	0.7	33	1.3
Harpacticoids	0.5–1.0	75	3.0	25	4.9	0.5–1.5	100	73.1	100	52.5
Peltidiids	0.8–1.0	25	0.2	25	0.3	0.8–1.0	67	5.6	50	8.0
Metis holothuriae	0.5	75	1.5	—	—	—	—	—	—	—
Tegastids	0.5	25	0.8	25	0.3	0.5	50	2.7	17	0.5
Undetermined	0.6–1.0	25	0.5	25	4.3	0.6–1.5	83	64.8	100	44.0
Mysidaceans	2.0–4.0	100	109.8	100	12.8	1.5–7.0	100	6679.9	100	5810.2
Anisomysis spp.[§]	4.0	25	5.0	—	—	4.0–7.0	100	235.3	100	206.5
Pseudanchialina inermis	—	—	—	—	—	3.0–4.0	67	848.3	83	1346.7
Siriella spp.[¶]	—	—	—	—	—	5.0–7.0	33	1.7	50	3.0
Gastrosaccus bengalensis	—	—	—	—	—	4.0	17	1.3	17	4.0
Undetermined juveniles	0–4.0	100	104.8	100	12.8	1.5–3.0	100	5593.3	100	4250.0
Cumaceans	—	—	—	—	—	1.0–2.0	100	135.3	83	18.2
Tanaidaceans	0.5–2.5	50	2.0	—	—	1.5–4.0	100	19.4	50	6.9
Leptochelia sp.	0.5–2.5	25	1.0	—	—	2.0–4.0	100	17.7	50	4.4
Tanais sp.	1.0	25	0.7	—	—	1.5	17	—	50	0.5
Undetermined	1.0	25	0.3	—	—	1.5	33	1.7	17	2.0
Isopods	—	—	—	—	—	1.0–10.0	100	21.3	100	17.3
Epicaridean larvae	—	—	—	—	—	1.0–2.0	33	3.0	83	9.3
Gnathiid females and juveniles	—	—	—	—	—	2.0–3.0	100	17.0	50	8.0

TABLE 1 (*Continued*)

	DAY					NIGHT				
		STATION A (INTERMITTENT CURRENT) $N = 4$		STATION B (NO CURRENT) $N = 4$			STATION A (INTERMITTENT CURRENT) $N = 6$		STATION B (NO CURRENT) $N = 6$	
ORGANISM	SIZE (mm)	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.	SIZE (mm)	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.
Anthurids	—	—	—	—	—	4.0–10.0	33	0.3	—	—
Sphaeromatids	—	—	—	—	—	2.0	17	0.7	—	—
Cirolanids	—	—	—	—	—	1.5	17	0.3	—	—
Gammarideans	1.0–1.5	50	1.0	—	—	0.7–6.0	100	82.4	100	9.6
Synopia variabilis	—	—	—	—	—	2.0–4.0	17	—	50	3.2
Maera sp.	—	—	—	—	—	3.0–4.0	67	4.0	17	0.2
Aorids	—	—	—	—	—	1.5–2.5	50	57.0	—	—
Seven others[#]	1.5	25	0.5	—	—	2.0–6.0	67	3.4	33	0.4
Undetermined	1.0	25	0.5	—	—	0.7–5.0	100	18.0	50	5.8
Euphausiids	0.8	—	—	25	0.5	0.6–9.0	33	5.2	50	2.7
Calyptopis larvae	0.8	—	—	25	0.5	0.6–0.7	33	3.5	17	2.0
Pseudeuphausia latifrons	—	—	—	—	—	4.0–9.0	33	1.7	50	0.7
Natantian larvae	1.0–4.0	100	19.5	100	13.5	1.0–7.0	100	467.6	100	770.0
Natantian postlarvae	—	—	—	—	—	3.0–15.0	100	53.2	100	34.0
Ogyrides sp.	—	—	—	—	—	4.0	50	6.7	100	13.8
Alpheids	—	—	—	—	—	4.0–6.0	16	0.3	—	—
Other carideans	—	—	—	—	—	3.0–7.0	100	39.7	100	15.5
Lucifer sp.	—	—	—	—	—	8.0–13.0	67	6.2	33	4.7
Other penaeids	—	—	—	—	—	15.0	16	0.3	—	—
Zoeae	0.5–2.0	100	22.5	75	5.3	0.4–2.0	100	860.0	100	931.7
Megalopae	—	—	—	—	—	1.0–4.0	100	37.0	100	21.7
Chaetognaths[**]	3.0–8.0	75	13.5	25	0.5	4.0–31.0	83	124.7	100	103.0
Larvaceans	2.0–3.0	25	0.8	25	0.5	3.0–4.0	33	22.7	33	47.3
Fish eggs	0.5–3.0	100	131.0	100	136.3	0.5–3.0	100	197.3	100	288.3
Fish larvae	2.0–6.0	50	0.5	75	1.0	0.5–15.0	100	45.7	100	48.3
Miscellaneous[††]	—	—	6.5	—	3.8	—	—	30.9	—	14.4
$\bar{x}$ Zooplankton volume		0.5 ml		0.3 ml			10.6 ml		9.4 ml	
$\bar{x}$ Algae volume		10.7 ml		2.7 ml			1.6 ml		0.4 ml	
$\bar{x}$ Total		11.2 ml		3.0 ml			12.2 ml		9.8 ml	

[*] Includes taxa where mean number of individuals taken at any station day or night was greater than 0.5.

[†] We base our identification of *Discorbis* sp. on Cushman et al. (1954). Apparently this is a benthic form, as many individuals (not counted) were attached to the fragments of benthic algae in our collections. According to Myers (1943), *Discorbis* (and other genera) are the benthic stages of the planktonic *Tretomphalus* spp., but the nominal designation is retained here to emphasize the ecological distinction, which is more important to this study.

[‡] Other calanoids included *Acrocalanus monachus*, *Candacia* sp., *Centropages* sp., *Euchaeta rimana*, *Labidocera laevidentata*, *Pleuromamma abdominalis*, *P. xiphias*, *Pontellina plumata*, *Scolecithricella* sp., *Tortanus* sp., and *Undinula darwini*.

[§] Including *Anisomysis constricta*, *A. enewetakensis*, and *A. chessi* (Murano 1983).

[¶] Including *Siriella affinis* and *S. aequiremis*.

[#] Other gammarideans included *Cerodocus* sp., *Elasmopus* sp., *Ronco sosa*, amphilochids, amphithoids, leucothoids, and stenothoids.

[**] Chaetognaths included *Sagitta bedfordii*, *S. enflata*, *S. ferox*, *S. neglecta*, *S. oceania*, and *S. robusta* (Angeles Alvariño, fishery biologist, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038, pers. comm., April 1981).

[††] Miscellaneous forms taken in low numbers included hydromedusae, siphonophores, syphozoans, heteropods, pteropods, cephalopods, cladocerans, monstrilloid copepods, stomatopod larvae, hyperiid amphipods, pleuteus larvae, thaliaceans, and ascidian larvae.

TABLE 2

COPEPODS COLLECTED ABOVE THE LAGOON SHELF IN DAYLIGHT WITH NETS OF DIFFERENT MESH SIZE[*]

	0.333 MESH $N = 2$		0.165 MESH[†] $N = 2$	
TAXA	MEAN NO.	SIZE RANGE (MEAN)	MEAN NO. (ADJUSTED)	SIZE RANGE (MEAN)
Calanoids[‡]	17	0.7–1.3 (1.0)	310.0	0.3–1.0 (0.6)
Cyclopoids[§]	3	0.6–0.8 (0.7)	914.5	0.3–0.8 (0.4)
Harpacticoids[¶]	4	0.5–0.9 (0.6)	294.5	0.3–0.6 (0.4)

[*] Paired collections close to Station B during midafternoon, one with 0.333-mm mesh net in a 0.78-m^2 square frame, the other with a 0.165-mm mesh net in a 0.5-m circular frame. To make collections with the two net sizes equivalent, values given for the finer mesh are collected values times 3.1.

[†] Two additional collections with the finer mesh near Station A produced similar results but were not paired with the larger mesh and thus are not included here.

[‡] *Acartia negligens* and unidentified forms.

[§] *Corycaeus* sp. and *Oithona* sp.

[¶] *Tegastes* sp., *Metis holothuriae*, and unidentified forms.

FIGURE 2. Typical arrangement of the traps used to sample meroplankters that rise into the water column from the major substrata on the lagoon shelf at Enewetak Atoll. Left to right: rubble, sand, and reef.

Both diurnal and nocturnal conditions were sampled. Each daytime deployment of the three traps was paired with a deployment that sampled the same spots during the preceding or following night. Some of the day/night pairs of sets began with daytime collections, others with the nighttime collections. When starting with the daytime collections, we placed the traps in position between sunrise and 0800 hr and retrieved the nets between 1730 hr and sunset, leaving the bases in place. Upon retrieval, all materials were washed and then removed for preservation in 4% formaldehyde (as were all our plankton collections). The nets, with empty cod ends in place, were then reattached to the bases and left in place throughout the night. The following morning, again between sunrise and 0800 hr, the entire traps—nets and bases—were retrieved and the collected organisms preserved as before. This sequence was reversed when we had begun the day/night pair of sets with the night collection. After completing one pair of sets, we moved to a different location and repeated the procedure for the next pair of sets. Six paired sets were made in the vicinity of Station B. Of the six near Station A, four were made in locations periodically swept by currents and two were made in nearby waters sheltered from these currents. In all, 56 samples were taken. (Four reef collections were canceled—two day and two night—while that trap was repaired.) The trap collections were made during the same periods as were the water-column collections, described above, and thus encompassed the same range of tides (spring to neap) and lunar phases.

Our trap collections (Table 3) showed that organisms which entered the water column from the benthos did so primarily at night (Wilcoxon two-sample test: $Z = -6.28$, $p < 0.0001$). These benthos-related forms, including various polychaetes, ostracods, mysids, tanaids, isopods, amphipods, and carideans, have been variously referred to as demersal plankton (Alldredge and King 1977, 1980; Porter and Porter 1977), epibenthic plankton (McWilliam et al. 1981), and meroplankton (Williams and Bynum 1972; Hobson and Chess 1979; Robichaux et al. 1981). We consider the relatively few organisms trapped by day to be of uncertain, or at most minor, significance.

Generally, the organisms that entered the water column at night were more numerous in the trap collections from areas sheltered from currents. The 18 trap collections made at night in areas sheltered from currents took $\bar{x} = 635.9$ (SE 163.3) individuals of 93 taxa, whereas the ten trap collections made at night where intermittent currents flowed took $\bar{x} = 360.4$ (SE 82.7) of 69 taxa. Although this difference lacked significance (Wilcoxon two-sample test: $Z = -0.79$, $p = 0.215$), certain groups were far more numerous in the sheltered area. This was particularly true of mysidaceans ($\bar{x} = 106.7$; SE 57.7) in collections from the sheltered area, compared to $\bar{x} = 3.5$ (SE 1.8) from the current area (Wilcoxon two-sample test: $Z = -3.15$, $p < 0.001$). Although these data document a general trend, they are insufficient to relate the benthic shelter sites of particular species to the current patterns.

Although our samples lacked the sensitivity needed to define specific benthic microhabitats of the three broad categories sampled—reef, rubble, and sand—the largest numbers came from the reef. The eight collections made at night on reef substrata took $\bar{x} = 935.13$ (SE 315.9) individuals of 76 taxa compared to $\bar{x} = 643.9$ (SE 72.3) of 79 taxa in ten collections from rubble and $\bar{x} = 113.1$ (SE 16.6) of 59 taxa in ten collections from sand.

Our scheduled collections did not include samples of the mysids that we observed swarming at many places on the shelf during the day, especially in areas sheltered from currents. These aggregations occurred as dense balls close to patch reefs and as immense mats 50 to 100 cm thick close above open sand. (An unscheduled pass with our 0.333-mm mesh net through a small segment of one such aggregation netted approximately 60,000 individuals, all *Anisomysis* sp., 1.5 to 4 mm long.) At the same time, much smaller aggregations of mysids, generally consisting of larger individuals, frequently occurred close beneath the water's surface. (An unscheduled pass with our net through one such relatively small aggregation enveloped the entire group, capturing approximately 1900 individuals, 6 to 7 mm long, again all *Anisomysis*

TABLE 3

ORGANISMS COLLECTED IN THE BENTHIC TRAPS ON THE LAGOON SHELF AT ENEWETAK ATOLL, DAY AND NIGHT

	DAY			NIGHT		
TAXA	% OCCUR.	MEAN NO.	(SE)	% OCCUR.	MEAN NO.	(SE)
Foraminiferans	71	9.96	(2.99)	96	35.32	(8.80)
Tretomphalus sp.	68	8.04	(2.72)	93	16.57	(5.60)
Cymbaloporella sp.	25	1.50	(0.64)	61	15.61	(4.33)
Others (undet.)	18	0.43	(0.20)	61	3.14	(0.66)
Polychaetes	25	0.25	(0.08)	82	2.50	(0.38)
Opheliids	7	0.07	(0.05)	43	0.89	(0.27)
Others	18	0.18	(0.07)	71	1.61	(0.29)
Gastropods	25	4.21	(3.63)	96	6.25	(1.27)
Ostracods	4	0.11	(0.11)	86	4.43	(0.89)
Myodocopids	4	0.07	(0.07)	71	3.64	(0.93)
Podocopids	4	0.04	(0.04)	36	0.79	(0.28)
Calanoids	54	1.61	(0.74)	89	5.43	(1.03)
Paramisophria sp.	—	—	—	46	1.54	(0.42)
Others	54	1.61	(0.74)	79	3.89	(0.86)
Cyclopoids	7	0.14	(0.10)	25	0.36	(0.14)
Harpacticoids	61	1.64	(0.46)	100	42.5	(13.14)
Peltidiids	32	0.50	(0.16)	79	20.68	(6.85)
Tegastids	—	—	—	11	2.11	(1.93)
Others	50	1.14	(0.35)	96	19.71	(5.53)
Mysidaceans	—	—	—	82	69.82	(37.71)
Pseudanchialina inermis	—	—	—	46	1.93	(0.53)
Siriella spp.	—	—	—	21	1.14	(0.76)
Gastrosaccus bengalensis	—	—	—	29	0.64	(0.24)
Other adults	—	—	—	14	0.86	(0.65)
Juveniles	—	—	—	57	64.96	(37.25)
Cumaceans	—	—	—	89	5.46	(1.20)
Tanaidaceans	21	0.50	(0.23)	79	7.50	(1.95)
Leptochelia spp.	14	0.39	(0.23)	75	6.46	(1.60)
Tanais sp.	4	0.04	(0.04)	18	0.86	(0.47)
Others	4	0.07	(0.07)	18	0.18	(0.07)
Isopods	4	0.07	(0.07)	89	6.86	(1.24)
Epicaridean larvae	—	—	—	43	1.43	(0.28)
Gnathiid females and juveniles	—	—	—	54	3.68	(0.93)
Others	4	0.07	(0.07)	71	2.04	(0.42)
Gammarideans	25	0.25	(0.08)	96	13.54	(2.05)
Synopia variabilis	—	—	—	39	2.29	(0.89)
Maera spp.	4	0.04	(0.04)	36	0.68	(0.25)
Elasmopus sp.	—	—	—	18	0.50	(0.28)
Aorids	—	—	—	57	3.93	(1.39)
Amphilochids	—	—	—	11	0.18	(0.12)
Others	21	0.21	(0.08)	82	5.96	(1.02)
Natantians	32	0.79	(0.40)	100	225.47	(51.67)
Larvae	32	0.79	(0.40)	86	213.39	(51.96)
Alpheids	—	—	—	64	2.93	(0.84)
Other carideans	—	—	—	96	9.04	(1.24)
Penaeids	—	—	—	4	0.11	(0.11)
Reptantians	7	0.07	(0.05)	68	78.14	(36.69)
Zoeae	7	0.07	(0.05)	43	76.96	(36.65)
Megalopae	—	—	—	43	0.93	(0.26)
Others	—	—	—	21	0.25	(0.10)

TABLE 3 (*Continued*)

	DAY			NIGHT		
TAXA	% OCCUR.	MEAN NO.	(SE)	% OCCUR.	MEAN NO.	(SE)
Chaetognaths	—	—	—	50	1.61	(0.45)
Spadella legazpichessi	—	—	—	32	0.68	(0.26)
Others	—	—	—	32	0.93	(0.37)
Fish eggs	57	2.43	(0.56)	93	27.46	(6.13)
Fish larvae	—	—	—	32	2.54	(2.13)
Fishes, postlarvae*	—	—	—	25	0.36	(0.14)
Miscellaneous	39	0.61	(0.18)	71	2.00	(0.36)
Total mean number		22.64			537.54	

* Includes *Amphioxus*.

sp.) These aggregations dispersed at nightfall and reformed the following morning.

ZOOPLANKTON FROM THE OPEN SEA

The zooplankton that arrived above the shelf from the open sea outside the atoll were sampled from the flow of water that crossed the interisland reef at high tide (Station C, Figure 1). To make these collections, we used the same net as at the other stations, but here we mounted it alongside a skiff anchored on an inflowing current near its maximum flow. During the collections the water was about 1.5 m deep and was moving 45 to 84 cm/sec^{-1} (determined by a current meter), so the net, positioned just beneath the surface, sampled most of the water column. We varied the time the net was in the water—4.75 to 7.50 min—according to the water flow, so that the volume of water filtered approximated that filtered by each of the regular 10-min diver-controlled collections at the other sites. Because we had found earlier that nearshore zooplankters were most numerous in the water column on dark nights (Hobson and Chess 1976), our nocturnal collections were made during the new moon.

Each collection on the interisland reef at Station C was followed within 30 min by another collection directly downcurrent above the lagoon shelf. This second collection, made using the standard diver-controlled method, provided a basis for inferring the origin of certain zooplankters above the lagoon shelf. We reasoned that species which were more numerous in the cross-reef flow than above the shelf downcurrent were likely to be transients from outside the lagoon. (We expected that zooplankters in the shallow water crossing the reef would quickly disperse upon entering the deeper water behind the reef.) On the other hand, species that were few or absent in the waters coming into the lagoon, but numerous above the shelf directly downcurrent, were likely to be residents of the shelf or to have come from offshore in the lagoon.

The number of zooplankters carried over the reef from outside the atoll was much greater at night (Table 4), which was consistent with the nocturnal increase in numbers of zooplankton above the shelf. The nighttime flow carried $\bar{x}$ = 8208 zooplankters compared to $\bar{x}$ = 460 in the daytime flow (omitting the foraminiferan *Discorbis* sp.; see Table 1, footnote 2). Hence we concentrate on organisms arriving at night. Zooplankters that were numerous in the nocturnal reeftop flow, but which were at the same time considerably fewer above the shelf downcurrent (indicating a probable origin outside the atoll), included halocyprid ostracods, the calanoid *Undinula vulgaris*, the euphausid *Pseudeuphausia latifrons*, certain of the chaetognaths (which were not identified to species but probably included those listed in Table 1, footnote 7), and certain larvae, including natantians and zoeae. In comparison, zooplankters few or absent in the nocturnal reeftop flow, but at the same time

TABLE 4

ZOOPLANKTERS IN CURRENTS CROSSING THE INTERISLAND REEF COMPARED TO DOWNSTREAM ON THE LAGOON SHELF[*]

	DAY				NIGHT			
	REEFTOP $N = 2$		LAGOON SHELF $N = 2$		REEFTOP $N = 2$		LAGOON SHELF $N = 2$	
TAXA	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.
Foraminiferans	100	630.0	100	59.5	100	80.0	100	322.5
Tretomphalus sp.	100	66.5	100	37.0	100	54.5	100	215.0
Discorbis sp.	100	563.5	50	21.5	100	20.5	100	100.5
Cymbaloporella sp.	—	—	25	0.5	50	2.0	50	2.0
Globigerina sp.	—	—	50	0.5	50	1.5	50	4.0
Others	—	—	—	—	50	1.5	50	1.0
Siphonophores	—	—	50	0.5	50	1.5	50	8.0
Polychaetes	100	2.0	—	—	100	6.5	100	3.0
Opheliids	50	1.0	—	—	—	—	100	3.0
Nereid epitokes	—	—	—	—	100	5.0	—	—
Tomopteris sp.	—	—	—	—	50	1.5	—	—
Undetermined	50	1.0	—	—	—	—	—	—
Veligers	100	36.0	100	60.0	100	20.0	100	11.0
Ostracods	50	0.5	50	0.5	100	124.0	100	61.0
Cypridinaceans	50	0.5	50	0.5	50	2.0	100	49.0
Halocyprids	—	—	—	—	100	122.0	100	12.0
Calanoids	100	43.5	100	70.0	100	3592.5	100	1457.5
Acartia negligens	100	8.0	100	33.0	100	110.0	100	10.0
Undinula vulgaris	100	10.5	—	—	100	2605.0	100	1000.0
Calanopia minor	—	—	—	—	—	—	50	3.0
Lucicutia flavicornis	—	—	—	—	100	216.0	100	25.0
Ten others[†]	50	6.0	50	0.5	100	91.5	100	49.5
Undetermined	100	19.0	100	36.5	100	570.0	100	370.0
Cyclopoids	100	10.0	50	30.5	100	55.0	50	14.0
Corycaeus sp.	50	1.0	50	24.0	100	34.0	50	10.0
Oncaea sp.	100	8.5	50	6.0	—	—	—	—
Oithona sp.	—	—	—	—	50	15.0	50	4.0
Sapphirina sp.	50	0.5	50	0.5	50	4.0	—	—
Copilia sp.	—	—	—	—	50	2.0	—	—
Harpacticoids	100	8.0	50	2.5	50	4.0	100	34.0
Peltidiids	—	—	50	0.5	—	—	—	—
Metis holothuriae	—	—	50	2.0	—	—	—	—
Tegastids	—	—	—	—	50	4.0	50	4.0
Undetermined	100	8.0	—	—	—	—	100	30.0
Mysidaceans	50	4.0	100	185.0	50	4.0	100	2026.0
Anisomysis spp.	—	—	50	10.0	—	—	100	220.0
Pseudanchialina inermis	—	—	—	—	50	4.0	100	36.0
Gastrosaccus bengalensis	—	—	—	—	—	—	50	30.0
Juveniles	50	4.0	100	175.0	—	—	100	1740.0
Stomatopod larvae	—	—	—	—	100	420.0	100	118.0
Cumaceans	—	—	—	—	—	—	100	12.0
Tanaidaceans	100	5.0	50	3.5	—	—	100	16.0
Leptochelia sp.	100	5.0	50	2.0	—	—	100	8.0
Tanais sp.	—	—	50	1.5	—	—	50	8.0
Isopods	50	10.0	—	—	—	—	50	0.5
Epicaridean larvae	50	10.0	—	—	—	—	50	0.5
Gnathiid females and juveniles	—	—	—	—	—	—	—	—

TABLE 4 (*Continued*)

	DAY				NIGHT			
	REEFTOP $N = 2$		LAGOON SHELF $N = 2$		REEFTOP $N = 2$		LAGOON SHELF $N = 2$	
TAXA	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.	% OCCUR.	MEAN NO.
Gammarideans	50	1.5	100	2.0	100	6.0	100	33.0
Synopia variabilis	—	—	—	—	50	2.0	100	14.0
Maera sp.	50	1.0	—	—	50	2.0	100	1.0
Four others[‡]	50	0.5	50	1.0	—	—	100	4.0
Undetermined	—	—	50	1.0	50	2.0	100	14.0
Euphausiids	—	—	—	—	100	640.0	100	48.0
Pseudeuphausia latifrons	—	—	—	—	100	640.0	100	48.0
Natantian larvae	100	10.0	100	9.0	100	420.0	100	320.0
Natantian postlarvae	50	4.0	—	—	100	72.0	100	115.0
Ogyrides sp.	—	—	—	—	50	0.5	—	—
Alpheids	50	4.0	—	—	—	—	50	16.0
Other carideans	—	—	—	—	100	39.5	100	95.0
Lucifer sp.	—	—	—	—	100	32.0	50	4.0
Zoeae	100	44.0	100	33.0	100	1110.0	100	180.0
Megalopae	—	—	—	—	100	40.0	100	40.0
Chaetognaths	50	12.0	100	21.0	100	720.0	100	290.0
Larvaceans	—	—	50	1.5	50	24.0	50	4.0
Fish eggs	100	175.0	100	50.0	100	6200.0	100	230.0
Fish larvae	—	—	50	0.5	100	22.0	100	32.0
Miscellaneous[§]	—	—	—	3.5	—	86.7	—	4.6

[*] Includes taxa where mean number of individuals at either station, day or night, was greater than 1.0.

[†] Other calanoids included (* = reeftop; $^{+}$ = lagoon shelf): *Candacia* sp.$^{*+}$, *Centropages* sp.$^{+}$, *Euchaeta marina*$^{*+}$, *Labidocera laevidentata*$^{+}$, *Pleuromamma abdominalis*$^{*+}$, *P. xiphias*$^{*+}$, *Pontillina morii*$^{+}$, *P. plumata*$^{+}$, *Tortanus* sp.$^{*+}$, and *Undinula darwini*.

[‡] Other gammarideans included: *Leucothoe hyhelia*; *Prodocerus* sp.; an amphilochid (nighttime lagoon shelf); and *Seba* sp. (one individual, daytime, reeftop; not previously reported from Micronesia).

[§] Miscellaneous forms taken in low numbers included pteropods, cephalopods, cladocerans, cypris larvae, stomatopod larvae, hyperiids, insect (*Holobates* sp.), pluteus larvae, thaliaceans, and ascidian larvae.

abundant above the shelf downcurrent (indicating they had not arrived from outside the lagoon), included cypridinacean ostracods, mysidaceans, cumaceans, tanaids, and gammarideans. Significantly, these were species known from our benthic trap collections (Table 3) to include residents of the shelf that shelter on the substrate during the day.

ZOOPLANKTON FROM THE DEEPER WATER OF THE LAGOON

Probably zooplankters that moved over the lagoon shelf at night from the deeper waters of the lagoon advanced over a broad front. Presumably this was not a purposeful shelfward migration, but rather a net movement in that direction by some proportion of the population. We would expect it to be a result of dispersing in the surface waters after an ascent from the depths adjacent to the shelf. Although such an advance would be highly diffuse, and not directly measurable by our collecting methods, it seemed possible to develop inferential evidence that would identify some of the prominent organisms involved.

Having determined that the larger transients are above the shelf only at night, we reasoned that those from the deep lagoon would be numerous there during the day. To identify them, we established Station D about 1 km beyond the outer edge of the shelf, where the water was about 30 m deep. This site was selected after visual search, and random sampling, had determined that larger zooplankters were concentrated between depths of

9 and 15 m but were sparse or absent both above and below these depths. To sample, we pushed the same net used at the other stations along a course that led up and down through the depths where the zooplankters were concentrated. As a check on our visual impression that this concentration did not extend deeper (where zooplankters would be increasingly difficult to see), we then made a second collection 10 m below the first. Two weeks later we went directly to the same location, immediately found the concentrations at the same level as before, and repeated the collections.

Of species that were numerous above the lagoon shelf at night, but virtually absent in collections there by day (Table 1), only the calanoid *Undinula vulgaris* and chaetognaths were numerous in the daytime collections at Station D. These, however, were the richest taxa in those collections (other than various larval forms). The two collections (2 weeks apart) that sampled the concentration of zooplankters between depths of 10 and 15 m took 370 and 310 *Undinula vulgaris* (2–3 mm) and 240 and 840 chaetognaths (4–14 mm). *Undinula vulgaris* represented 14.9%, and chaetognaths 23.8%, of the nonlarvae in the two collections. On the other hand, neither *U. vulgaris* nor chaetognaths occurred in the two collections made 10 m deeper at the same time and place.

But even if we can assume that *U. vulgaris* and chaetognaths from the deep lagoon were among the transients above the shelf at night, there remained the problem of distinguishing them in the shelf zooplankton from others of the same species that, as determined from our collections above the interisland reef (Station C: Table 4), came from the open sea. This distinction is considered in the following discussion.

DISCUSSION

Although many zooplankters of about 1 mm or less were numerous above patch reefs on the lagoon shelf during both day and night, it was evident that the vast majority of those larger than about 1.5 mm were in the water column there only at night. Many of these larger individuals were shelf residents that by day were in or on shelf substrata, or in swarms close above these substrata, whereas others were transients from the open sea or from the deep lagoon. Here we make further distinctions between the residents and transients, while discussing how their ascent in the water column represented a general nocturnal vertical migration with subsequent dispersion in the surface waters. We also discuss how the resulting distribution was influenced by water currents. First, however, possible sources of sampling error are acknowledged.

Possible Sampling Error

Because our plankton collections were from relatively shallow water, some may have included strictly benthic forms that had been swept into the water column by turbulence, perhaps attached to algal fragments (for example, the foraminiferan *Discorbis* sp.). This contamination would most likely occur in our traps or when our plankton nets sampled close to the sea floor, but we believe that it had little or no effect on our conclusions. Drifting plant fragments were far more abundant by day (Table 1), for example, and the zooplankters upon which we base our analysis were consistently more numerous in our collections at night. Probably some strictly benthic forms climbed the inner sides of our traps and entered the collections (Hobson and Chess 1979; Robichaux et al. 1981), but these would not include organisms important to our analysis, which were also taken in the water column by our plankton nets. Furthermore, confidence in our data is increased by the consistency of results from these two different collection methods—nets and traps—combined with direct observations of many of the organisms *in situ*.

Shelf Residents Among the Larger Zooplankters

Certain zooplankters above the shelf at night were identified as residents when captured by our traps as they emerged from shelf substrata. Prominent among them were various polychaetes, ostracods, mysids, tanaids, isopods, amphipods, and carideans. Possibly some individuals of these species also came from benthic habitats in deeper parts of the lagoon, but there was no evidence in the samples from the reeftop flow (Station C) that any came from outside the atoll.

The residents also included those species that aggregate by day in dense swarms close to benthic substrata. Although at Enewetak we noted this behavior only among mysids, especially *Anisomysis* spp., we have seen it among copepods elsewhere (Hobson and Chess 1979 and unpublished data). Daytime swarms of both mysids and copepods are widespread in tropical reef communities (Emery 1968; Hamner and Carleton 1979).

Probably the residents also included *Calanopia minor*, although the diel distribution of this calanoid remains somewhat uncertain. It was the most numerous copepod in nocturnal collections above that part of the shelf sheltered from currents, but was much scarcer where intermittent currents flowed and, with the exception of just a single individual, was not taken by us during the day (Table 1). It has been reported that many individuals of this species spend the day in the sediments of the Enewetak Lagoon (Barnett 1967), as is the case with a congener, *C. americana*, at Bermuda (Clarke 1934). So even though we failed to collect *C. minor* in our benthic traps, we nonetheless believe that at least many of those above the shelf at night are in the shelf sediments by day and therefore are residents of that habitat. Many of those we collected were taken at about last evening light—the same time that many known residents first appear in the water column—so these could not have come from far away, especially as the currents that might have accelerated an arrival from greater distances were lacking where they were most abundant. Some *C. minor* may have arrived above the shelf at night from the deeper waters of the lagoon—Barnett (1967) found this species abundant at the base of the water column in the mid-lagoon during the day. But there is no evidence that any come from the open sea, as none were among the zooplankton arriving in the reeftop flow. Similarly, a congener, *C. elliptica*, was the major calanoid collected by Sale et al. (1976) in a lagoon of the Great Barrier Reef, Australia, but was not among the calanoids they collected in open water outside that lagoon. And in collections by Clarke (1934) at Bermuda, *C. americana* was the dominant copepod in bays and harbors but was absent in collections from the ocean outside (except in sharply decreasing numbers close to the mouths of the enclosed waters).

EFFECTS OF CURRENTS: Certainly the resident zooplankters would benefit from means to prevent being carried away from their home grounds by water currents. To consider the vulnerability of the residents to currents, however, requires a measure of their swimming abilities. This measure is lacking for the species considered here, but rough approximations can be based on swimming speeds of comparable species measured elsewhere. Of mysids, which included perhaps the strongest swimmers among the zooplankters considered here, those species that have been studied traveled up to about 15 $\mathrm{cm/sec^{-1}}$ (Steven 1961; Clutter 1969). Because this would not be enough to overcome even the relatively weak currents (up to 25 $\mathrm{cm/sec^{-1}}$) that regularly flowed through our study area, we would expect the current patterns to have a strong influence on the distribution of these zooplankters.

Those residents that are benthonic during part of the diel cycle—including harpacticoids, mysidaceans, cumaceans, tanaids, isopods, and gammarideans—probably have close ties to specific benthic habitats and avoid currents that would carry them away. Certainly the nocturnal distribution of *Calanopia minor* indicated that it favored areas of reduced current. But when all those collected by our benthic traps are considered (Table 3), the numbers collected were not significantly greater in the sheltered area than in the current area. Apparently, many with ties to benthic habitats tolerated these weak currents, perhaps by taking advantage of eddies or by limiting their planktonic modes to periods of slack water. We suspect, however, that they would have been less successful adjusting to conditions where currents were much stronger and, in fact, they were sparsely distributed where currents exceeding 1 m/sec^{-1} flow into the lagoon through the deeper channels (Hobson and Chess 1978). Further evidence that these forms do, in fact, avoid currents exists in their absence in the reeftop flow (Table 4). Considering their prominence in the nocturnal plankton above the shelf (Table 1, 3, and 4), there must have been at least some representatives of these taxa in the nocturnal plankton above reefs outside the lagoon. Although we would expect them to be considerably fewer in that surge-swept habitat than in the lagoon, some should have been carried in the reeftop flow—unless they avoided this current. Significantly, many larvae of these same taxa, including zoeae, megalopae, and natantian larvae, were numerous in the nocturnal reeftop flow (Table 4) and clearly did not avoid this current. At least many of these larvae are benthonic by day (Table 3), but unlike their adults they apparently lacked close ties to specific benthic habitats. In fact, probably at least many of them benefited from currents as adaptive means to disperse.

Those resident mysids that swarmed close to the shelf floor during the day were numerous only in areas sheltered from currents. All seemed to be *Anisomysis* spp., and members of this genus were not among the mysids that sheltered in or on the substrate (Table 3). Apparently, therefore, these species do not have the capacity to avoid intermittent currents by sheltering there. The relatively few mysid swarms that occurred in areas of intermittent current were sheltered in the lee of patch reefs when these currents flowed (Hobson and Chess 1978).

Other resident zooplankters that have been reported to swarm close to benthic substrata by day—including certain cyclopoids such as *Oithona* spp. and calanoids, such as *Acartia* spp. (Emery 1968; Hamner and Carleton 1979; Hobson and Chess 1979)—may similarly avoid currents. Although the reports cited did not consider the distributions of these species relative to currents, they did contain evidence that currents are avoided. For example, there is frequent mention of copepod swarms being in such places as "between coral heads or other sheltered locations" (Emery 1968:295) and "most pronounced ... in sheltered embayments" (Hamner and Carleton 1979). Similarly, when Hamner and Carleton once saw copepods in small swarms on a windward reef slope, they considered them to be in an unusual location. They also considered it noteworthy that in one place where a 5 cm/sec^{-1} current flowed, small swarms of *Acartia* maintained station in eddies downcurrent of boulders.

Transients Above the Lagoon Shelf at Night

In considering as transients those species that appeared above the shelf from the ocean outside the atoll, or from the deeper waters of the lagoon, we are mostly concerned with holoplankters that perform diel vertical migrations in open water. The arrival of these species in the shallows at night appears related to a general ascent into the surface waters after dark, a phenomenon widespread among the zooplankters of Pacific atolls (Johnson 1949; Hobson and Chess 1973), as it is among zooplankton in general (Cushing 1951). Presumably many of the zooplankters that rise into surface water from open-ocean depths windward and upcurrent of the atoll are carried into the lagoon when these waters wash over the interisland reef. And many of the zooplankters that disperse into the surface waters from lagoon depths would be expected to spread over the adjacent shelf unless blocked by currents from that direction (Hobson and Chess 1978).

The major transient zooplankter above the lagoon shelf was the calanoid *Undinula vulgaris*. This species was the most widespread and generally abundant zooplankter in that habitat at night, but it was sparsely distributed there during the day (Table 1). *Undinula vulgaris* has been considered a lagoon endemic that only incidentally occurs in the open sea (Johnson 1949), but while we found it a major species among the deep-lagoon zooplankters during the day, its numbers in water that flowed into the lagoon from outside the atoll at night (Table 4) indicate that it also was abundant in the surrounding ocean. Reports from other areas support this view. For example, in the plankton collections made by Sale et al. (1976) inside and outside a lagoon on the Barrier Reef, *U. vulgaris* was a major species only in the collections from outside. And while this widely ranging species is known to have neritic tendencies (Grice 1961) and was not among the calanoids collected by Chiba et al. (1955) at oceanic stations in the Micronesia area, it has been found far from land (Owre and Foyo 1967). Furthermore, in their daytime collections at Enewetak, Gerber and Marshall (1974:816) found the shallows above the lagoon shelf (including a station near our study site) "largely devoid of *U. vulgaris*," when at the same time they collected it abundantly in the mid-lagoon and in a deep passage from the sea. So whether in the lagoon or in the surrounding ocean, *U. vulgaris* seems to be a species of deeper water rather than the nearshore shallows.

EFFECT OF CURRENTS: The transient zooplankters, unlike the residents, did not show adaptive behavior related specifically to the currents that flowed over the shelf. Perhaps this should been expected, because it seems unlikely that these open-water species would have acquired adaptive responses to characteristics of shallow-water habitats. Instead, the currents appeared to influence them simply by accelerating their movements downstream and blocking their movements upstream. This apparently straightforward relationship between their movements and current provides means to judge whether certain open-water transients that occurred above the shelf during the night were likely to have come from the open sea or from the deeper waters of the lagoon.

Our consideration of this point is highly conjectural, but it illustrates some of the variables that should influence the distribution of transient zooplankters above the shelf. The analysis is limited to *U. vulgaris*, which would seem the best choice to represent the variety of transients above the shelf after dark. Among the many open-sea species prominent in the reeftop flow (Table 4), only *U. vulgaris* was identified as abundant and widespread above the shelf. And of the species that were abundant above the shelf at night, but much fewer there during the day (Table 1), only *U. vulgaris* was identified as numerous at our daytime collecting site offshore in the lagoon (Station D). Chaetognaths seemed to have a similar pattern of occurrence, but the six or more species in our samples (Table 1, footnote 7) were not distinguished in the individual collections.

To determine which of the many *U. vulgaris* above the shelf at night came from the open sea, and which were more likely to have come from the deep lagoon, we assumed they would have arrived from those opposite directions in numbers relative to differing conditions of tide, current, and time of night. We reasoned that individuals from each of the two directions could be distinguished by collections that sampled a diverse combination of these variables. Thus certain of the collections at Stations A and B sampled on the higher tides, when currents flowing across the interisland reef should have carried zooplankters from outside the atoll but blocked the shelfward advance of zooplankters from the deeper waters of the lagoon. And certain other collections sampled the lower tides, when the exposed interisland reef blocked the flow of water and the zooplankters from outside the atoll, but when, in the absence of this flow, the zooplankters from the deep lagoon should have been free to spread over the shelf. Obviously the length of time the condition had been in force should have been important. The time of night should have been important, too. While zooplankters from the open sea should have arrived shortly after sunset when the currents that carried them were flowing, zooplankters from offshore in the lagoon, being without assisted transport, could not have spread to the inner regions of the shelf until later during the night, even under the most favorable conditions.

The nocturnal occurrences of *U. vulgaris* above the shelf at Stations A and B showed a clear pattern (Table 5). The large number at Station A during high tide (collections A_2 and A_4) undoubtedly arrived in the currents that flowed across the interisland reef from the open sea at this time. Not only did these currents provide transport from that direction; they also blocked shelfward movements by zooplankters from the deep lagoon. On the other hand, because these currents were large-

TABLE 5

NUMBERS OF *Undinula vulgaris* COLLECTED AT NIGHT UNDER VARYING ENVIRONMENTAL CIRCUMSTANCES ABOVE THE LAGOON SHELF AT ENEWETAK ATOLL

	STATION A (INTERMITTENT CURRENT)						STATION B (NO CURRENT)					
	HIGH TIDE		LOW TIDE, EARLY		LOW TIDE, LATE		HIGH TIDE		LOW TIDE, EARLY		LOW TIDE, LATE	
SPECIES AND CONDITIONS	A2	A4	A1	A6	A3	A5	B2	B4	B1	B6	B3	B5
Species												
Undinula vulgaris	400	170	10	0	960	28	24	72	8	0	180	600
Conditions												
Date	5/30	6/4	5/27	6/4	6/2	6/4	5/30	6/4	5/27	6/4	6/2	6/4
Time[*]	0500	0130	2330	2115	0330	0445	0430	0100	2300	2045	0300	0415
Tide height[†]	3.7	3.2	1.1	2.2	2.3	2.5	3.5	3.3	1.2	2.2	2.3	2.6
Tide direction[‡]	F4.5	E1.1	E5.5	F2.0	F0.3	E4.2	F4.0	E0.5	E5.0	F1.5	E5.5	E3.8
Current (cm^{-1})	0[§]	15	8	0	0	10	0	0	0	0	0	0
Moon[¶]	0.29x	0.50x	0.07x	0.57p	0.43x	0.50x	0.29x	0.50x	0.07x	0.57p	0.43x	0.50x

[*] Sunrise on these dates was at 0653 hr; sunset at 1932–1934 hr (calculated from sunrise and sunset table, Tide Tables 1979, National Ocean Survey, NOAA, U.S. Dept. of Commerce).

[†] Values represent height of the tide (in feet) above mean lower low water, as calculated from Tide Tables 1979, Dept. of Commerce. During our 3 weeks at Enewetak mean high tide was 3.8; mean low tide was 1.5.

[‡] E = ebb tide; F = flood tide. Numeral is hours that tidal phase had been in effect (e.g., E5.5 = tide had been ebbing for 5.5 hr).

[§] Moderate current passing within 10 m of collection site. (See text for description of current patterns at this station.)

[¶] Numeral represents moon phase, where 0.00 = new moon and 1.00 = full moon; x = moon not visible during observations (owing to time of night or cloud cover); p = moon visible.

ly blocked at Station B, it is not surprising that there were relatively few *U. vulgaris* at this site during the same high tides (collections B$_2$ and B$_4$). Although the origin of these few remains uncertain, the lagoonward drift noted above the shelf offshore from this site during high tide would have been enough to prevent a shelfward advance by *U. vulgaris* from the deep lagoon. Although this drift was estimated as only a few cm/sec^{-1}, presumably this would have been too much for *U. vulgaris* to swim against. Although there are no data on the swimming capabilities of this species, individuals of another calanoid, *Metridia pacifica*, 2–3 mm long and therefore comparable in size to *U. vulgaris*, move 0.8 to 1.2 cm/sec^{-1}—and this is considered fast for a copepod (Enright 1977).

On the other hand, the *U. vulgaris* that were abundant at both Stations A and B during low tide late at night probably came from the deep lagoon (Table 5: low tide, late collections A$_3$, A$_5$, B$_3$, B$_5$), because at this time the currents that had carried zooplankters onto the shelf from the open sea during high tide were shut off by the exposed interisland reef. That so few were present at both stations during low tide earlier in the night (Table 5: low tide, early collections A$_1$, A$_6$, B$_1$, B$_6$) can be explained by the time they would have required to spread over the shelf after rising into the surface waters at nightfall—even those that rose out of the depths close to the shelf's edge. Being without benefit of the current that accelerated the movement of individuals from the open sea, it must have taken *U. vulgaris* and most others at least several hours to reach the inner regions of the shelf (based on the swimming speed of a similar species, cited above), and this would have been with a direct, purposeful advance, which seems unlikely to have occurred. More likely it took them considerably longer.

The relatively low numbers of *U. vulgaris* in collection A$_5$ despite the late hour may relate to the 10 cm/sec^{-1} current that was running against their advance at the time (Table 5: low late tide); as noted in the Methods section, even during low tide the trade winds or seas sometimes drove enough water across the interisland reef to generate currents on the shelf. The relatively few *U. vulgaris* in this collection certainly did not swim against a 10 cm/sec^{-1} current, but they may have arrived above the shelf before the current gained strength or may have benefited from a nearby eddy. Also, they may have been carried in wind-driven water that crossed the reef from the open sea at low tide, or among others that entered the lagoon from the open sea during high tide earlier that night.

Possibly the increased numbers of *U. vulgaris* during late low water represented an accumulation of individuals that had been carried into the lagoon from the open sea during high water earlier that night. But this would not explain the comparatively low numbers collected at the sheltered site during late high water (when conditions for an arrival from seaward would seem more favorable). In our opinion, the combination of data and circumstances arrayed in Table 5 is best explained if, in the absence of currents at night, large numbers of zooplankters from offshore in the lagoon spread over the lagoon shelf.

The Larger Zooplankters at Dawn

The routes taken by the larger zooplankters to arrive above the shelf at night seem reasonably clear. But what happened to them at dawn? Those residents with close ties to benthic substrata would have had no problem returning to their benthic habitats if, as it appears, they were able to stay above these habitats during their noctural excursions into the water column. But what about *U. vulgaris* and other transients that arrived from the open sea or the deeper waters of the lagoon? Certainly there was no return for them over the interisland reef to the open sea. Where the lagoonward currents flowed, as at the exposed site (Station A), many, if not most, may have been carried off the shelf into the deep lagoon before dawn. But in the absence of such currents, as at the sheltered site (Station B), we would expect at least many to have been stranded above the shelf at daybreak. It seems unlikely that they migrated across the shelf before descending into the depths beyond the dropoff, because in their normal deep-water habitat the appropriate behavior at daybreak for most is a direct descent. Possibly they descended directly to the shelf floor to become mixed and unrecognized in the detritus that accumulated on the sand. It seems more likely, however, that with daybreak in these unfamiliar shallows at least many of the open-sea zooplankters became increasingly vulnerable to planktivorous fishes and were consumed. Although *U. vulgaris* was scarce in the diurnal plankton collections made above the shelf (Table 1), the earliest of these collections was made at 1030 hr, and by that time many could have been removed by diurnal planktivores. Significantly, 2–3-mm individuals of this species were the major prey of the diurnal planktivore *Chromis carulea* at the sheltered site during midday (Hobson and Chess, unpublished data).

Thus the experience of open-water transients that occur above the lagoon shelf at night would seem much like that suggested for vertically migrating oceanic zooplankters that reportedly are carried above coastal shelves during their nocturnal occurrences in the surface waters. The reports suggest that these zooplankters risk being trapped by the seafloor in these coastal shallows during attempts to regain their normal daytime depths, and that this situation renders them vulnerable to predators (Isaacs and Schwartzlose 1965; Pereyra et al. 1969; Clarke 1984).

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